Photosynthetic Characteristics of *Veratrum californicum* in Varied Greenhouse Environments

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ABSTRACT

Corn lily or California false hellebore (*Veratrum californicum* Durand), a perennial species native to the western United States, produces several alkaloid compounds. A derivative of these alkaloid compounds, primarily veratramine and cyclopamine, shows promise as a therapeutic agent for treatment of a variety of tumor types. Here we report the first study of corn lily cultivated in greenhouse. Growth response of corn lily was examined under two light levels (ambient and supplemental), two fertilization types (20 N-4.4 P-16.6 K Peat-lite special and 15N-2.2P-12.5K CalMag special) at 100-mg·L^{-1} total nitrogen, and three irrigation cycles [sub-irrigation every day (wet), every third day (dry), and hand watering]. Net CO_2 assimilation rate (Pn) and transpiration rate (ET) of corn lily grown under supplemental light were 11.0% and 44.7%, respectively, higher than those under ambient light. The Pn and ET of corn lily grown with the *wet* irrigation cycle increased by 15.2% and 29.4%, respectively, when compared with the Pn and ET of plants grown under the *dry* irrigation cycle. Corn lily grown *wet* with supplemental light had the highest average Pn of 8.55 ± 0.36 µmol·m^{-2}·s^{-1}, while plants grown under ambient light with hand watering had the lower average Pn of 6.52 ± 0.48 µmol·m^{-2}·s^{-1}. The highest mean ET recorded for corn lily was 4.97 ± 0.17 mmol·m^{-2}·s^{-1} when plants were grown dry with supplemental light, while the lowest ET recorded was 2.51 ± 0.18 mmol $m^{-2}s^{-1}$ when plants were grown under ambient light and hand watered. In corn lily, photosynthesis was increased with supplemental light and when volumetric water content remained above 44%. The water use efficiency of corn lily may be low, as water is not normally limiting in the natural environment where corn lily grows.

INTRODUCTION

Corn lily (*Veratrum californicum* Durand; Melanthiaceae family) is a poisonous, herbaceous perennial, facultative wetland species in its native habitat range within the Rocky Mountains and mountains of western North America (Niehaus et al., 1984; USDA, 2011). The *Veratrum* genus consists of 27 species (Ferguson, 2010; Liao et al., 2007; Zomlefer et al., 2003).

The corn lily plant, also known as California false hellebore, can grow from 1 to 2 m in height with a cornstalk-like stem (Niehaus et al., 1984). The plant is attractive with large, broadly ovate-elliptical leaves and with dense panicles of creamy-white flowers (James et al., 2004; Keeler and Binns, 1971). Corn lily has been used in herbal medicine for a relatively long time and has potential pharmaceutical uses (Boericke, 1927). The activity of the plant alkaloids, such as cyclopamine, manifests as birth defects, such as cyclopia and holoprosencephaly on grazing pregnant animals (James et al., 2004; Keeler and Binns, 1971). Recently, cyclopamine and its derivatives have been examined as promising therapeutic agents for the treatment of tumors arising from activation of the hedgehog-signaling pathway (Berman et al., 2002; Chen et al., 2002; James et al., 2004; Taipale and Beachy, 2001; Wang, 1990; Watkins et al., 2003). In particular,

Infinity Pharmaceuticals (Cambridge, MA) has developed a novel semisynthetic analogue of cyclopamine with substantially improved pharmaceutical properties and potency (Tremblay et al., 2009).

The endemic distribution of corn lily ranges from 1000 to 3400 m above sea level. Under these conditions, growth is only possible during the snow-free months. Most corn lilies thrive in rich, deep, moisture-retentive soil in partial shade to full sun, tolerate the wet soil conditions, and are typically found colonizing moist alpine meadows and woodlands via underground rhizomes. To date, harvesting rhizomes from existing wild colonies is the main source of the pharmaceutically active compounds that are used in the synthesis of an anti-cancer medication. The colonies do not recover quickly (>7 years) after harvest, even if replanted with mature bulbs and rhizome divisions collected on site. A sustainable cultivation system would be beneficial, both to maintain wild colonies and to ensure availability of adequate quantities of alkaloid compounds for therapeutic purposes.

Few ornamental plant production nurseries cultivate corn lily, suggesting that the plant may not be easy to grow using typical production means. Propagation via seed cultivation is limited because seed viability rapidly decreases, prolonged cold stratification is required for germination, and the seedlings are small and grow slowly (Ferguson, 2010; Taylor, 1956; Williams and Cronin, 1968). Moreover, corn lilies produce seed only intermittently (Taylor, 1956), and seedlings can take 7-10 years to attain maturity and flower (Ferguson, 2010; Taylor, 1956). Divisions of rhizomes along with a bulb can develop roots in a sandy soil in cold frame (Huxley, 1992). This technique, however, requires harvesting large number of rhizomes from wild colonies. Tissue culture offers an alternative to conventional propagation, and cultivation of micropropagated plant material in the greenhouse or field would help to preserve wild populations of corn lily while ensuring adequate supplies of plant tissue for therapeutic purposes.

Little information is available on the cultivation and physiological adaptation of corn lily in a greenhouse setting. Therefore, our objective was to characterize plant photosynthetic parameters as influenced by environmental and cultural conditions in the greenhouse, documenting the influence of irrigation, fertilization, and light on the growth and primary metabolism of corn lily.

MATERIALS AND METHODS

Plant material. Rhizomes of corn lily (*Veratrum californicu* Durand) were harvested from a wild population in Heber valley, UT, on September 9, and received in Clemson, SC, on September 10. Upon arrival, the rhizomes, each with one bulb, were potted into 19.7-cm-diamter plastic containers (3.8 L) filled with Fafard 3B mix [45% Canadian sphagnum peat moss, 25% processed pine bark, 15% perlite, 15% vermiculite, starter nutrients (40-230 $mg \cdot L^{-1}$ N; 5-30 $mg \cdot L^{-1}$ P; 40-200 $mg \cdot L^{-1}$ K, Ca, and S; 25-80 $mg \cdot L^{-1}$ Mg), wetting agent, dolomitic limestone; Conrad Fafard, Inc., Anderson, SC] and drenched with 330 $mg \cdot L^{-1}$ Subdue® (25.1% metalaxyl: *N*-(2, 6-dimethyl-phenyl)-*N*-(methoxyacetyl) alanine methyl ester, 74.9% inert ingredients; Syngenta Crop Protection, Inc., Greensboro, NC) to prevent root rot. Subdue® was reapplied on April 12.

After potting, the corn lily rhizomes were stored in the dark at 10 °C and 70% relative humidity (RH) for two weeks (pretreatment) and then at 5 °C and 65% RH for approximately five months in a controlled environment room (Model# 120-208; Climate Technologies, Inc., Laytonsville, MD) in the Clemson University Biosystems Research Complex. All rhizomes were moved into a glass-glazed greenhouse on February 10, and watered by hand twice a week until March 15. Thereafter, irrigation treatments were applied through the end of the experiment on May 23.

Experimental design. The experimental design was a 2 × 3 × 2 factorial with light, irrigation, and fertilizer treatments with eight replicates per subirrigation treatment and six replicates per hand-watering treatment. A total of 88 plants were included in the experiment.

Light. Supplemental light treatments were introduced February 17. Half of the plants remained under ambient light conditions; while the remaining plants received 12 h of supplemental light (0600 to 1800 Eastern Standard Time) from 1000-W metal halide lamps (Agrosun Gold; Hydrofarm, Inc., Medley, FL) placed 1.5 m above the bench. Average daily light intensity during the treatment ranged from 249.6 to 1342.2 $\mu mols \cdot m^{-2} \cdot s^{-1}$

for the supplemental light treatment in comparison with ambient light treatment that ranged from 53.9 to 824.3 μmols·m^{-2}·s^{-1}. The photoperiod ranged from 11 to 14 h throughout the experiment.

Irrigation. Irrigation treatments included two subirrigation treatments (wet and dry) and one hand-watered treatment (hand). The hand-watered plants were irrigated with 150 mL solution per container, applied to the medium surface when container volumetric water content (VWC) of the substrate fell below 30%. Substrate moisture was monitored daily at 1600 with values from 10-HS soil moisture sensors (Decagon Devices, Inc., Pullman, WA) inserted into the substrate of two containers per treatment were recorded for the duration of the experiment.

The subirrigation treatments were managed using an automatic subirrigation system. The subirrigation system consisted of four Dayton® utility pumps (Model # FMP-50-P, W.W. Granger, Inc., Lake Forest, IL) regulated by relays and an Orbit® signature timer (Orbit Irrigation Products, Inc., Bountiful, Utah), and drained using four Honeywell valves (Model No. V8043E1137, Honeywell Inc., Golden Valley, MN). The pumps were connected to four 190 L tanks (Rubbermaid Commercial Products LLC, Winchester, VA) that were kept dark under black plastic and held solubilized nutrients for fertilizer treatments. Irrigation water was then pumped, according to fertilizer treatment, into eight trays (58.5 cm × 48.3 cm × 10.2 cm) that held our subirrigation treatment experimental plant units.

Ebb and flood subirrigation events were initiated at night to reduce algal growth from exposure to light. Pumps cycled on at 1800 every day (wet) or every third day (dry) and ran for five minutes to fill the trays to 2.8 ± 0.4 cm high with water from the tanks, supplying approximately 110 ± 17 mL of water per container with each irrigation cycle. Drain valves switched open at 0600 every day to drain all water in trays. Each irrigation cycle brought soil moisture to container capacity (>96%).

The two fertilizer treatments consisted of a peat-lite special fertilizer supplied at 100 mg·L^{-1} total N (20N−4.4P−16.6K, Scotts Peters Professionals, Marysville, OH) and a Cal-Mag special fertilizer supplied at 100 mg·L^{-1} total N (15N−2.2P−12.5K, Scotts Peters Excel, Marysville, OH). Each treatment was either applied using the above subirrigation system or via hand watering. Tank solutions (pH = 5.6 ± 0.4; EC = 0.75 ± 0.1 mS·cm^{-1}) were refreshed on March 25, April 12, and April 27.

Environment monitoring. An ECD dataworker (ECD, Inc., Milwaukie, OR) recorded canopy air temperature hourly. Greenhouse temperatures were 25.5 ± 5.0°C (day) and 18.3 ± 3.6°C (night). Canopy level photosynthetic photon flux (PPF) was monitored hourly with LI-190 Quantum sensors (LI-COR® Biosciences, Lincoln, NE) and a LI-1400 data logger (LI-COR® Biosciences, Lincoln, NE). Daily light integral was calculated.

Photosynthetic measurements. To determine the photosynthetic saturation point, the diurnal net CO_2 assimilation rate (Pn), transpiration rate (ET), and leaf temperature (L_T) from 0600 to 2000 on March 24 were measured using the CIRAS-2 portable photosynthesis system (PP Systems International, Inc., Amesbury, MA) with a PLC6 broad leaf cuvette. To determine optimum timing for measuring maximal Pn, ET, and PPF rates, four healthy plants grown under ambient light and with a *wet* irrigation treatment (53.3 ± 3.2% VWC) were selected and measured for method development.

The fifth fully expanded leaf from the top of an individual plant was clamped inside the leaf cuvette. In all cases, temperature and water vapor pressure in the cuvette were kept at near ambient conditions, while CO_2 level was maintained from 358 to 379 μmol·mol^{-1}. Photosynthetically active radiation (PAR) was measured using a LI-COR radiometer (Model: LI-189; LI-COR® Biosciences, Lincoln, NE) and detected with LI-190 Quantum sensors (LI-COR® Biosciences, Lincoln, NE) concurrently with leaf gas exchange measurement. Net CO_2 assimilation rate, ET, and PPF rates reached their maximum between 1200 and 1400.

Leaf gas exchange in all treatments was monitored from 1200 to 1400 on March 30, April 11, April 22, and April 28, all cloudless days. In each treatment, the fifth fully expanded leaf of two plants were labeled and measured. In all measurements, the temperature in the cuvette was near ambient (34 ± 2 °C), water vapor pressure ranged from 67-75%, and CO_2 concentration was 362 ± 6.7 μmol·mol^{-1}. Plant height, from the bulb stem plate to the top of the shoot, and number of leaves (length > 3 cm) were measured on March 3, March 15, March 29, April 14, and May 23. In early April, we noted the formation of new bulbs inside the current year's stalk, and new bulbs swelled enough

to split the outer scales of the current year bulb. Bulb diameter was recorded on April 7 and again on May 23, at the experiment's conclusion.

Statistical analyses. Analysis of variance was done on all data using JMP v 9.0 (Statistical Analysis Systems, Cary, N.C.). Means were separated using Tukey's HSD. Treatment differences were significant if $P < 0.05$. Light saturation points were calculated using the equations generated from polynomial regression models.

RESULTS

Photosynthetic photon flux, measured at the canopy level of the corn lily plants, reached maximum values around 1300 (Figure 1). Photosynthetic photon flux at evaluation dates remained well above the light saturation point for corn lily, around 1000 µmol m^{-2} s^{-1} for both light treatments between 1200 and 1400. Leaf temperature (L_T) was highest around 1400 (Figure 2).

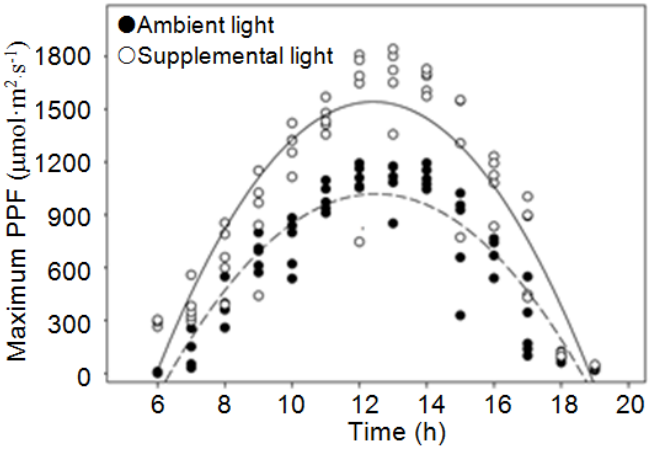

Figure 1. Diurnal photosynthetic photon flux measured at canopy level on March 24, March 30, April 11, April 22, and April 28, 2010.

Corn lily Pn and ET rates exhibited a similar diurnal pattern to L_T (Figure 2A-C). In the early morning, Pn, ET, and PPF rates were low and increased gradually until a maximum was reached between 1300 and 1400. After this peak, the Pn, ET, and PPF rates decreased until late afternoon. Both Pn ($P < 0.0001$, $r^2 = 0.79$) and ET ($P < 0.0001$, $r^2=0.73$) correlated strongly with changes in L_T. The L_T of corn lily was influenced by light intensity ($P < 0.0001$, $r^2 = 0.71$), and light saturation was reached at 1000 µmol m^{-2}·s^{-1} (Figure 2D). Corn lily Pn increased quadratically with light intensity ($P < 0.0001$, $r^2 = 0.83$) and the Pn saturation point was reached at a PPF of about 1000 µmol·m^{-2}·s^{-1} (Figure 2E). Light intensity influenced the transpiration rate ($P < 0.0001$, $r^2 = 0.47$). A maximum ET rate, however, was not defined (Figure 2F). Since light and temperature co-varied, the possibility exists that light saturation of Pn was related to temperature saturation when the leaves could no longer be cooled by increased rates of evapotranspiration.

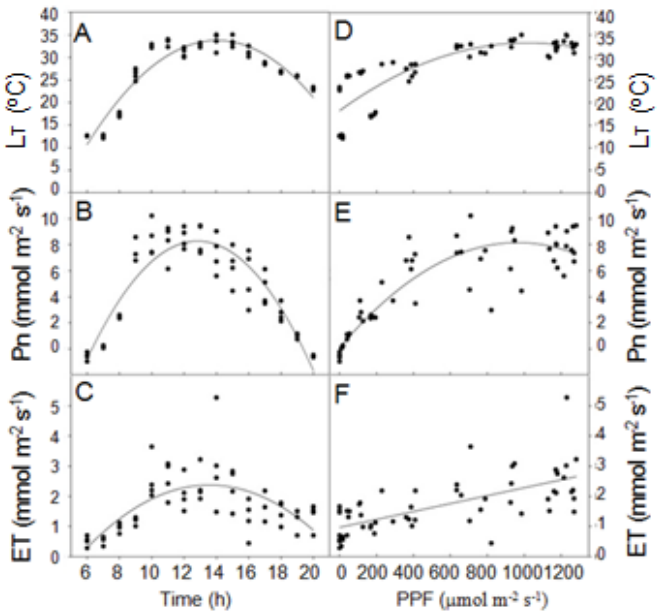

Figure 2. Diurnal changes in (A) leaf temperature (L_T), (B) net CO_2 assimilation rate (Pn), and (C) transpiration rate (ET) with these variables plotted against photosynthetic photon flux (PPF) (D,E, & F).

Measured from 0600 to 2000 on March 24, using four healthy plants grown under ambient light with the wet irrigation treatment.
Quadratic regression lines:
A = L_T=23.676+0.745 • time-0.356 • (time-13)2, r^2=0.89
B = P_n=9.107-0.064 • time-0.194 • (time-13), r^2=0.85
C = ET=1.829+0.041 • time-0.036 • (time-13)2, r^2=0.46
D = L_T=22.595+0.014 • PPF-1.455 •1 0-5 • (PPF -547.539)^2, r^2=0.71
E = Pn=2.696+0.007 • PPF-8.7041 • 0-6 • (PPF-547.539)^2, r^2 = 0.83
F = Linear regression line between PPF and ET, ET = 0.968+ 0.001 • PPF, r^2 = 0.47

Substrate VWC fluctuated greatly among irrigation treatments before April 20 Figure 3). After April 20, some plants within each treatment began to undergo senescence and the differences in soil moisture between the light treatments became less pronounced. Natural senescence may have reduced plant demand for water, thus the smaller fluctuations in soil VWC between irrigation events.

The net CO_2 assimilation rate and ET were consistent over the experiment evaluation period of March 30 to April 28 (Table 1). The light and irrigation treatments significantly impacted both Pn and ET. Neither Pn nor ET was influenced by fertilizer

type. Since no differences in fertilizer response were noted, data were pooled for analyses of light and irrigation treatment effects. Pn and ET rates were 11.0% and 44.7% higher, respectively, when grown under supplemental light as compared with plants grown under ambient light (Figure 4).

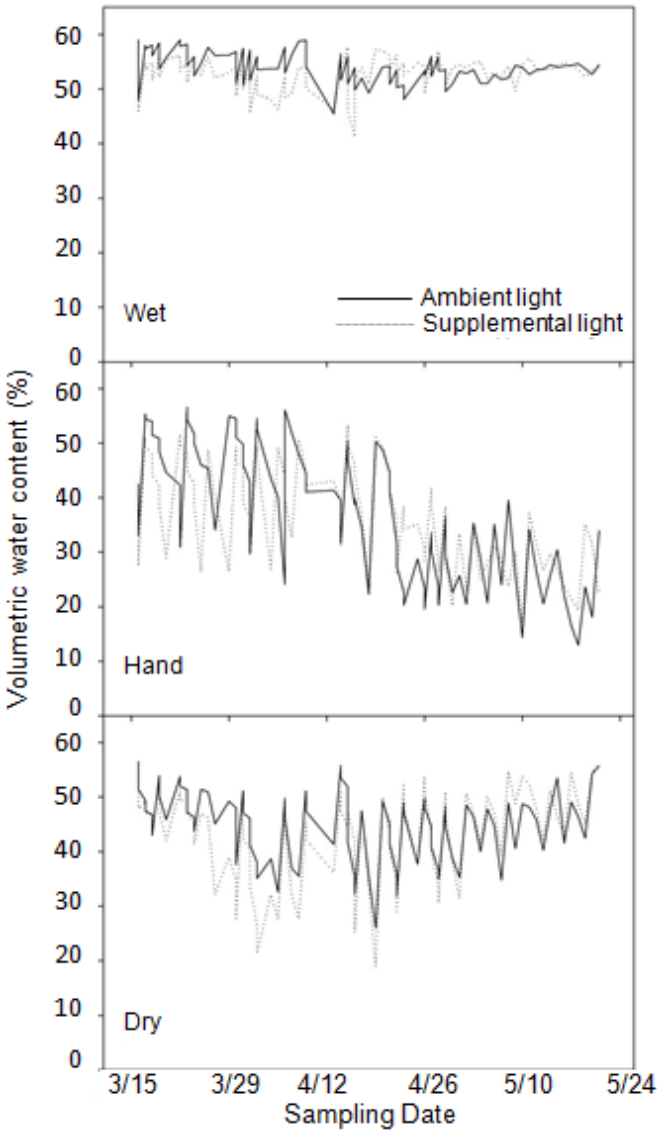

Figure 3. Water content of irrigated substrate during course of experiment.
Measurements were made at 1600 daily on two replicate samples per watering treatment.
Wet = subirrigation daily, average VWC = 53.4±3.0%
Hand = hand watering, average VWC=36.8±10.9%
Dry = subirrigation every third day; average VWC=44.0±7.6%
Ambient light - daily integral was 13.6±0.6 mol m^{-2} d^{-1}
Supplemental light- daily integral was 26.2±1.1 mol m^{-2} d^{-1}

The light and irrigation treatments significantly impacted both Pn and ET. Fertilizer type did not influence either Pn or ET. As no differences in response parameters were noted for fertilizer treatment, data were pooled for analyses of light and irrigation treatment effects. Corn lily Pn and ET rates were 11.0% and 44.7% higher, respectively, when grown under supplemental light as compared with plants grown under ambient light (Figure 4).

Table 1. Analysis of variance summary for corn lily development growing in a modified environment.

Source	Analysis of variance[1]				
	Pn	ET	Height	Number of leaves	Bulb size
Date	ns[2]	ns	***	***	***
Light	*	***	**	*	ns
Irrigation	*	***	ns	ns	ns
Fertilizer	ns	ns	ns	ns	ns
Interactions	ns	ns	ns	ns	ns

[1]Pn = assimilation rate, ET = transpiration rate,
[2]ns, *, **, *** = nonsignificant and significant at $P < 0.05$, 0.01, and 0.001, respectively.

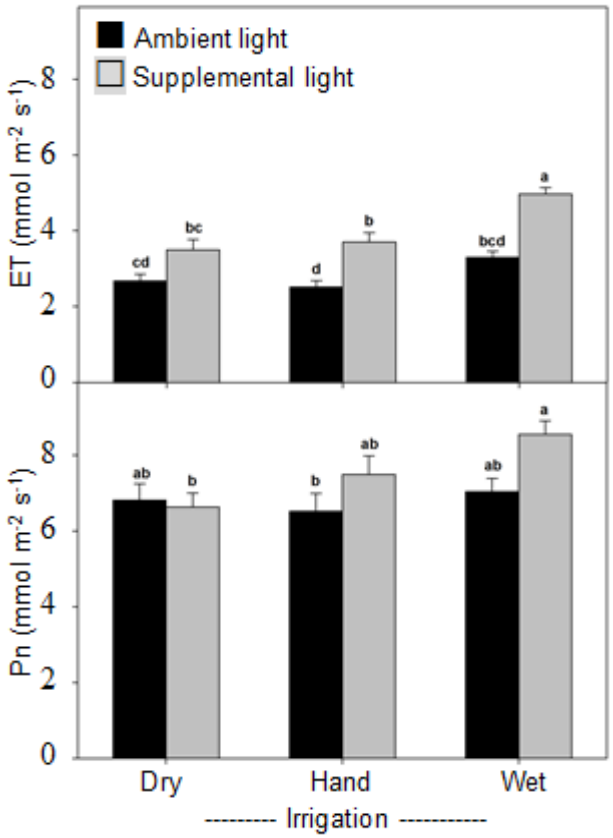

Figure 4. Net CO_2 assimilation rate (Pn) and transpiration rate (ET) on corn lily under two light and three irrigation treatments.
Irrigation treatments were as indicated in Figure 3.
Data, recorded on March 30 and April 11, 22, and 28, were pooled as no significant differences were detected among the dates. Different letters among treatments for each response variable indicate that significant differences ($P < 0.05$) were detected using Tukey's HSD mean separation. Vertical error bars represent the standard error of the mean.

The wet treatment increased the Pn and ET of corn lily by 15.2% and 29.4%, respectively, compared with the dry treatment. The only significant treatment effect on Pn was between corn lily plants grown with the supplemental light and wet treatments (8.55 ± 0.36 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and hand watered corn lily plants grown under ambient light or dry irrigated corn lily plants grown with supplemental light (6.52 ± 0.48 $\mu mol \cdot m^{-2} \cdot s^{-1}$) (Figure 4). All other Pn responses did not differ statistically among treatments. These results suggest that photosynthesis was more efficient when water was non-limiting (wet) and high light levels (supplemental) were present. The highest mean ET for corn lily was observed in the wet treatment with supplemental light (4.97 ± 0.17 $mmol \cdot m^{-2} \cdot s^{-1}$) while the lowest mean was 2.51 ± 0.18 $mmol \cdot m^{-2} \cdot s^{-1}$ when plants grew under ambient light and were hand watered.

During harvest from the native field site, 8 of 88 of bulbs were damaged. Mechanical abrasion of the outer scales of leaves appeared as ragged edges on some leaf margins. During the experiment, 32 of 88 plants succumbed to *Pythium* root rot. Malodorous tissue softened and collapsed. These plants were excluded from the data analysis, including all measurements that were conducted prior to the symptomatic detection of disease. Scorched foliage was observed on some of the corn lily that lived throughout the experiment.

Corn lily plants grew vigorously in the greenhouse for at least 70 days. By May 21, approximately 57.1% plants were in senescence. Plants grown with supplemental light initiated senescence earlier than those grown with ambient light (P = 0.03). This may be attributed to higher Pn of corn lily grown with supplemental light (Pn = 7.46 ± 0.25 $\mu mol \cdot m^{-2} \cdot s^{-1}$) in comparison with those grown under ambient light (Pn = 6.86 ± 0.23 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Bulb size increased significantly with time, but no difference was observed among any treatments (Table 1). On average, bulb diameter was 25.9 ± 0.5 mm on April 7 and 33.7 ± 0.79 mm on May 23. Bulb size increased about 30.1 ± 1.8% over 50 days.

Plants grew continuously during the first few weeks of the experiment, however, stalk elongation slowed and essentially ceased by April 20 (Figure 5). While plant height was influenced by light, neither fertilizer nor irrigation had any affect. At harvest, plant height ranged from 12.5 to 44.2 cm, which was smaller than wild populations (1 to 2 m).

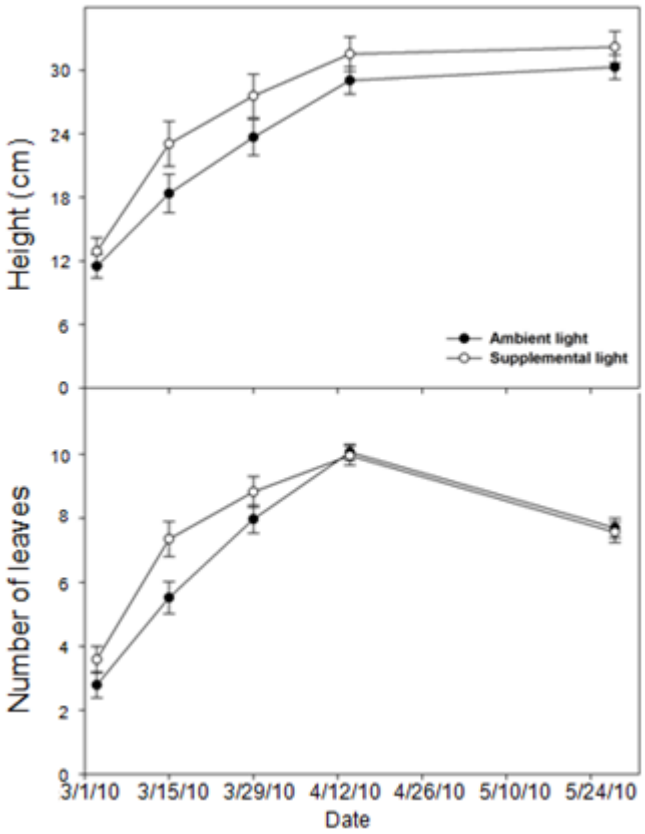

Figure 5. Corn lily plant height and number of leaves from stem plate to shoot tip.

Leaf numbers, counted on March 3, 5, 15, 29, April 14, and May 23, were initially impacted by supplemental light, but this effect was lost as plant height plateaued. Older leaves at plant base that had senesced or become necrotic were not counted after April 20. Data were pooled by ambient and supplemental light as no significant differences were detected from the fertilizer or irrigation treatmens.

Leaf number was impacted by light and date (Table 1, Figure 5). Supplemental light initially enhanced leaf number, perhaps by impacting the rate of elongation and expansion. By April 14, when height plateaued, leaf number no longer differed significantly among light treatments. The irrigation and fertilizer treatments did not significantly impact number of leaves. Corn lily senescence began around April 20, and any leaves that senesced after that date were not included in subsequent leaf numbers reported.

DISCUSSION

Photosynthetic rates of corn lily can be compared with other perennial species with similar morphology. The Pn of corn lily leaves reached

saturation when the PPF reached 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$, much higher than that of container-grown *Lilium longiflorum* Thunb. 'Nellie White' in which saturation occurs at 700 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Wang, 1990). The maximum Pn recorded for corn lily was 8 $\mu mol \cdot m^{-2} \cdot s^{-1}$, similar to *V. nigrum* L. (8.2 $\mu mol \cdot m^{-2} \cdot s^{-1}$) (He et al., 2008) and lower than *V. album* L. subsp. Oxysepalum Hulten (above 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$) (Tani and Kudo, 2006). The PPF of the corn lily is also much higher than the 4.5-6.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ reported for *Lilium* 'Oriental Hybrids' (Chang et al., 2008), or *Sagittaria lancifolia* L., another facultative wetland plant species with a PPF reported to be 2.7 - 6.7 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Lindau and Delaune, 2000), and twice that of the 4.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ Pn rate reported for *Zantedeschia aethiopica* (L.) Spreng. (Yiotis and Manetas, 2010). In addition, Fernandez et al. (1999) reported that the Pn of *Canna* × *generalis* L.H. Bail., *Iris* L. × 'Charjoys Jan', and *Pontederia cordata* L. ranged from 4 to 12 $\mu mol \cdot m^{-2} \cdot s^{-1}$, 3 to 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and 8 to 17 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. Our measurements showed similar photosynthetic rates between corn lily and *Canna* species. Both *Canna* sp. are considered facultative wetland species.

The higher Pn of Corn lily grown with supplemental light corresponds with research on *Lycoris longituba* Y.C. Hsu & G.J. Fan (Meng et al., 2008), where a high irradiance level increased net CO_2 assimilation rate. In deciduous forests, all *V. album* leaves show higher net CO_2 assimilation rates before leaf development in the tree-canopy, and the assimilation rates decrease rapidly with progressing tree-canopy closure (Tani and Kudo, 2006). These results may partially explain the reason corn lily grown with supplemental light senesced earlier in our study.

Carbohydrate storage theories propose that once a perennial organ is renewed and filled with carbohydrates, sink activity decreases and leaf senescence is induced (Lapointe, 2001). Sink-limited growth has been reported in *Crocus vernus* (L.) Hill (Badri et al., 2007) and *Helianthus tuberosus* L. (Schubert and Feuerle, 1997). In our experiment, new bulbs were produced, but bulb size at the conclusion of the experiment did not differ among treatments. A faster rate of bulb carbohydrate filling would result in reaching the sink limitation stage earlier. Thus, the higher net carbon assimilation rate of corn lily plants grown with supplemental light may have accelerated the rate of carbon storage and resulted in a faster reduction of carbohydrate sink demand, driving accelerated leaf senescence. In contrast, the bulb-filling rate of *Erythronium americanum* Ker Gawl has been shown to be dependent on the bulb cell elongation rate, rather than carbon availability (Gutjahr and Lapointe, 2008). Further studies relating leaf senescence and cell size, gas exchange rates, and nutrient concentrations may yield a clearer answer to the question of leaf senescence initiation.

Plants only partially affected by *Pythium* could undergo earlier senescence because *Pythium* has been shown to negatively impact photosynthesis and to restrict transpiration (Johnstone et al., 2004, 2005). In the current study, any excess variability in modeled data created by *Pythium* infection would most likely be contained within the random error unexplained by model main effects. Scorched foliage was observed on some of the corn lilies that lived throughout the experiment. Leaf scorching is commonly noted for many *Veratrum* species, especially when grown in dryer soils in full sun conditions (Ferguson, 2010).

Corn lily plants were taller with more leaves early in the season when grown with supplemental light. Plant height and leaf number, however, were reduced compared with those of wild populations. This reduction in leaf numbers was likely caused by root damage during field harvest. The greenhouse culture also had smaller differences in day and night temperatures compared with diurnal temperature differences in field grown corn lily.

In conclusion, corn lily plants had higher net photosynthetic rates with supplemental light and when their VWC remained, on average, above 44%. When adequate water and light levels were supplied, maximal Pn and ET rates were achieved, and the negative impacts of increased L_T and water stress were avoided. These stresses may decrease carbohydrate storage in corn lily. In their natural environment, corn lily plants grow with high PPF and adequate moisture. Supplying these two factors may be critical to more efficient production of corn lily in a greenhouse setting.

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